

A preliminary review of *Dennyus* (Mallophaga: Menoponidae)  
parasitic on swiftlets

by

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SUMMARY

A new subgenus is described for the species of *Dennyus* Neumann, 1906 parasitic on the avian genus *Collocalia* G. R. Gray. Redescriptions of two known species are provided; there is one new synonym; and five new species are described.

INTRODUCTION

The Mallophagan genus *Dennyus* Neumann, 1906 is confined in its known distribution to the swifts (Aves: Apodidae). I have for some time been engaged upon a study of the *Dennyus* from Old World hosts; the New World species are presently enjoying the attentions of workers elsewhere (Parsons & Collins, in preparation).

Two previous attempts have been made to subdivide *Dennyus*; *Takamatsuia* Uchida, 1926 was erected for *T. major* Uchida, 1926 and *Ctenodennyus* Ewing, 1930 for *C. spiniger* Ewing, 1930. Both genera were placed in synonymy to *Dennyus* by Hopkins & Clay (1952). In my opinion, these groups constitute useful subgeneric divisions, and a consideration of *Dennyus sens. strict.*, *Takamatsuia* and *Ctenodennyus* (in part) from Old World hosts will form the basis of a future paper.

The purpose of this contribution is to describe a new subgenus, the species of which are confined in their known distribution to the genus *Collocalia*, commonly known as "swiftlets". *Collocalia* is an exclusively Old World genus, and considerable difficulty has been experienced by ornithologists in settling the taxonomy of the genus; as expressed by Mayr (1937): "Every author who has ever worked with these small swiftlets of the Indo-Australian region will contend that their classification presents the most difficult problem in the taxonomy of birds. The members of this genus live in large or small colonies, frequently in inaccessible caves, and every population is slightly different from the next one. They are difficult to collect and not one of the museums of the world has adequate material. To make matters worse, most of the species are of practically the same dull sooty gray coloration with almost the same development of structural characters . . ."

The Mallophaga of *Collocalia* have never been examined in detail, and at the time of writing only two species of *Dennyus* have been described from swiftlets (a third described species has proved to be a synonym of the first). The material available to me is far from adequate for anything like a reasonable understanding of the species which occur on *Collocalia*, but it has been possible to clear up some doubtful points and present

some new observations which may be of use to other workers. It is hoped that ornithologists working with swiftlets will endeavour to collect ectoparasites, for the Mallophaga may in time prove to be useful as an aid to deciding taxonomic affinities in the group.

All lice studied were cleared and mounted on slides. Measurements, made with an ocular micrometer, are given in millimetres. A value in parenthesis following a statement of range represents the mean (means of setal counts have been corrected to the nearest whole number). The host nomenclature follows that of Peters (1940), which incorporates the work of Mayr (1937), but special regard has also been paid to Medway's recent classification, which is based on field characters of echolocation ability and nest construction (Medway, 1966). Because of the difficult nature of host identification, it should be borne in mind that certain host names in this paper may prove upon further investigation to be erroneous, particularly in those cases when only a few specimens are available from the alleged host.

Terminology used in the descriptions follows that of Clay (1969) as closely as possible. "Tergocentrals" are defined as the row of setae between (but not including) the stout seta on each side of tergite I (considered as postspiracular seta I in this paper) and the rows of setae between (but not including) the postspiracular seta and its associated slender inner seta on each side of II–VIII. The sternal setae may be divided into marginal (*m*) and anterior (*a*) series; additionally on V and VI there are lateral brushes of setae, the marginal components of which are not included in the marginal setal counts for these sternites.

The following abbreviations have been used to indicate collections from which material was examined: BMNH—British Museum (Natural History), London; GBT—Mr Gordon B. Thompson, Cambridge, England; KCE—Dr K. C. Emerson, Arlington, Virginia, U.S.A.; USNM—United States National Museum, Washington.

### *COLLODENNYUS* subgen. nov.

Type-species: *Dennys distinctus* Ferris, 1916.

DISTRIBUTION. On present knowledge, confined to the avian genus *Collocalia* G. R. Gray.

DEFINITION. Menoponidae with the following combination of characters. *Head* without notch or slit in dorso-lateral margin; ventral truncate-ovoid excavation with thickened anterior rim in dorsal margin of head anterior to eyes; without sclerotized processes arising near base of maxillary palpi; forehead truncate (figs 3 and 19), never smoothly rounded; temporal carinae well-developed, gular plate not horseshoe-shaped. Alveoli of dorsal head setae 26 and 27 not closely associated; *dhs* 18 absent, 23 present and anterior to 22; *dhs* 24 and 25 minute, 26, 27, 29 and 31 long and stout; 28 short; 30 medium and slender. 1 short, 1 medium setae between *dhs* 29 and 31. *Thorax* with 1 pair central pronotal setae, lateral pronotal lobes with 2 short, 1 long setae; 3 + 3 marginal pronotal setae. Prosternal plate well developed, 2 short setae anteriorly, never more than 2 additional medium setae on plate. Anterior mesonotal setae 2, marginal mesonotal setae 1 + 1, all minute. Mesosternum with 2 short anterior setae, posterior row of 2–5 medium setae. Anterior metanotal setae 3 + 3. No claws on 1st tarsi; thick brushes of setae ventrally on 3rd femora. *Abdomen* without anterior tergal

setae except for usual minute pair on I and II. Postspiracular setae long on I–VIII; a slender seta mediad to each postspiracular on II–VIII, absent on I. Terminal segment dorsally with 2 long stout setae each side with 1 minute seta between alveoli; 1 minute or 1–3 short setae mediad to this group. Sternite I reduced, represented by narrow plate between 3rd coxae, never more than 2 medium setae on this segment. Sternites II–VIII in male and II–VI in female are discrete central plates; II bordered anteriorly and laterally by a sclerotized “plate”, 2 + 2 short setae laterally each side; V and VI with lateral brushes of stout setae. In female, VII is fused with following sternites to form a subgenital plate; posterior corners of this plate always with 4 + 4 medium setae; middle part of plate with standard arrangement of 2 + 4 + 2 medium setae.

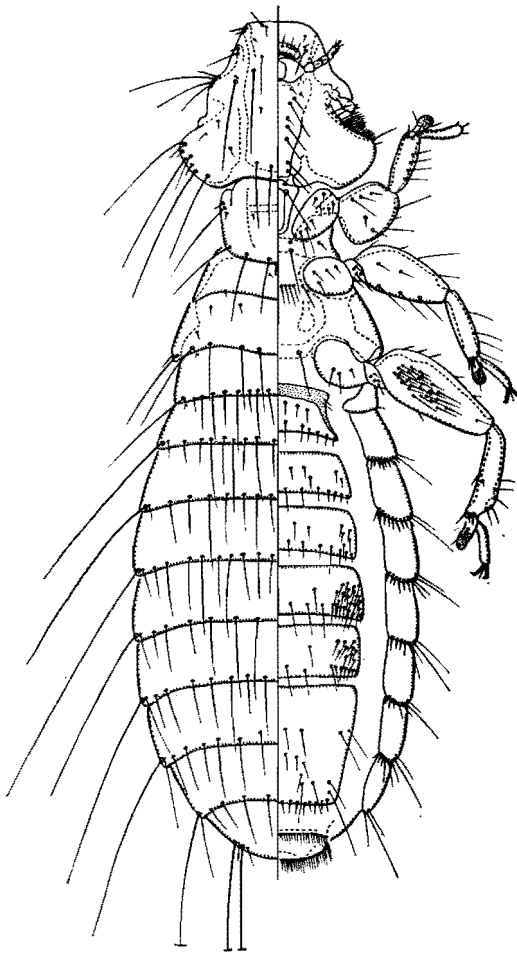


Fig. 1. *Dennysus* (*Collodennys*) *distinctus* Ferris, 1916. Female, dorsal/ventral view.

## Discussion

The well-developed temporal carinae and shape of gular plate separates *Dennys* from *Eureum*. Both are distinguished from *Myrsidea* by the excavation in the dorsolateral margin of the head; more than 2 central prosternal setae; *dhs* 23 present; 1 pair central pronotal setae present. *Collodennys* is separated from all other *Dennys* by the shape of the forehead (never smoothly rounded), the prosternal chaetotaxy (never more than 4 setae), the chaetotaxy of sternite I (never more than 2 setae) and by the absence of claws on the first pair of tarsi.

Within *Collodennys* two species-groups may be distinguished by the shape and chaetotaxy of the head. In the *distinctus* species-group the lateral margin of the forehead between *dhs* 8 and 4-5 is almost straight; *dhs* 2 and 3 are short, subequal; 5 is short and slender; 13 medium, reaching beyond the alveoli of 14 and 15 (see fig. 3). In the *thompsoni* species-group the lateral margin between *dhs* 8 and 4-5 is strongly concave; 2 is short; 3 minute; 5 stout and peg-like; 13 short, just reaching alveolus of 16 (see fig. 19).

### THE *distinctus* SPECIES-GROUP

*Dennys* (*Collodennys*) *distinctus* Ferris, 1916, figs 1-7

***Dennys distinctus*** Ferris, 1916, *Can. Ent.* 48(9):310, fig. 15

Type-host: *Collocalia* sp. (= *Collocalia esculenta linchi*)

***Dennys orientalis*** Büttiker, 1954, *Acta trop.* 11(2):160, fig. 5, **syn. nov.**

Type-host: *Collocalia esculenta stresemanni*

All quantitative data are based on a sample of 10♂♂ and 10♀♀.

**FEMALE.** General appearance and chaetotaxy as in fig. 1. Number and position of dorsal head setae as in fig. 3. Important setae: 2 and 3 subequal; 4 short and slender; 5 minute to short; 13 medium, reaching beyond alveoli of 14-15. 4 mesosternal setae (5 and 6 in some specimens); 9-13(10) central metasternal, 10-12(11) metanotal marginal setae.

**Postspiraculars.** Long on I-VIII; seta associated with postspiracular on II-VIII short and slender on II, increasing in length on succeeding tergites.

**Pleural chaetotaxy.** 1 spine on I; II-VIII always have (dorsal to ventral) 1 short, 1 medium seta; additionally up to 9 spines on II and III; on succeeding pleurites there are fewer additional setae (8-5 on IV-VII), and also there is progressive replacement of spines with short slender setae. VIII has only 1 additional slender seta (total, 3 on VIII). This arrangement of pleural setae is found throughout *Collodennys* (with some minor variation).

**Tergocentrals.** I, 15-19(16); II, 15-18(17); III, 14-19(17); IV, 14-18(16); V, 12-16(14); VI, 11-14(13); VII, 9-12(11); VIII, 7-9(8). Terminal segment dorsally with 2 long and stout, 2 minute setae.

**Ventral chaetotaxy.** II, 10-14(12) *m*, 4-8(6) *a* (see fig. 5); III, 12-16(14) *m*, 5-9(7) *a*; IV, 14-17(15) *m*, 16-18(14) *a*; V, 5-7(6) *m*, 0-5(3) *a*, lateral brushes 20-35; VI, 4-6(4) *m*, 0-5(3) *a*, lateral brushes 15-20. Vulval margin 12-18(14) short setae; middle part of subgenital plate 2+2 laterally (exceptionally 3 on 1 side), 4 medially (exceptionally 5); posterior corners with usual 4+4; additionally, a central group of 6-8 (8) short setae. Anal corona with shorter setae ventrally.

**MALE.** Characters of head, thorax and pleurites as for female; 8-10(10) metanotal marginal setae. Abdomen as in fig. 2; postspiraculars on VIII markedly stout.

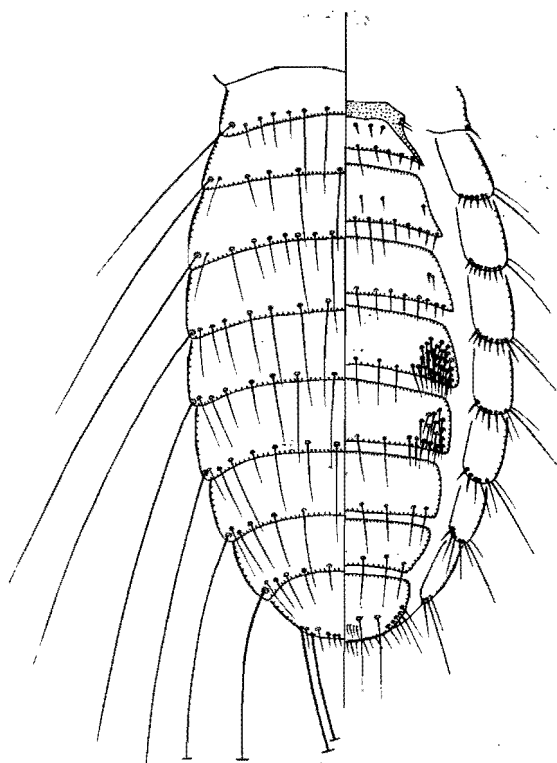


Fig. 2. *Dennyus (Collodennyus) distinctus* Ferris, 1916. Male abdomen, dorsal/ventral view.

*Tergocentrals.* I, 9-12(11); II, 10-14(12); III, 11-16(14); IV, 11-15(13); V, 10-14(12); VI, 10-12(11); VII, 9-11(10); VIII, 8. Terminal segment laterally as for female; 6-8 dorsal anal setae.

*Ventral chaetotaxy.* II, 7-12(8) *m*, 3-6(5) *a* (see fig. 4); III, 9-12(10) *m*, 3-7(6) *a*; IV, 10-13(11) *m*, 6-9(7) *a*; V, 4-6(6) *m*, 0-3(1) *a*, lateral brushes 25-30; VI, 3-4(4) *m*, 0-1(0) *a*, lateral brushes 15-20; VII, 8-10(8) *m*, usually arranged 2+4+2; VIII, 6 *m*. Terminal segment, 4 central submarginal setae, 17-20(19) marginal, those medial short and forming a ventral anal row, longer laterally and encroaching on to ventral part of segment; 6-8(6) internal anal setae. Genital armature as in fig. 6; sclerite as in fig. 7.

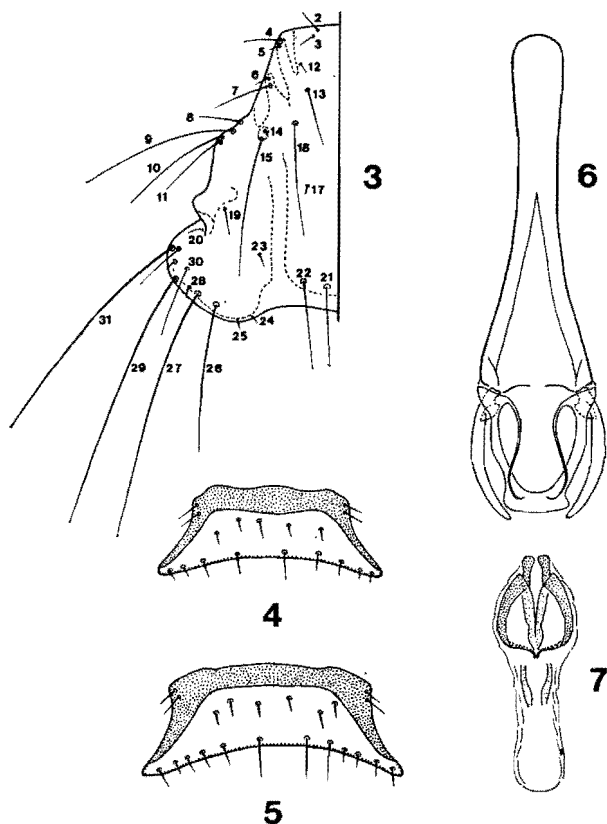
#### DIMENSIONS.

	<i>Female</i>	<i>Male</i>
Preocular width . . . . .	0.41-0.42 (0.42)	0.40-0.41 (0.40)
Temple width . . . . .	0.52-0.56 (0.55)	0.53-0.55 (0.54)
Head length . . . . .	0.43-0.46 (0.45)	0.42-0.44 (0.43)
Total length . . . . .	2.3-2.5 (2.5)	2.1-2.2 (2.2)

LECTOTYPE of *Dennyus distinctus*, ♀ ex *Collocalia* sp., Samarang, Java (E. Jacobson).

PARALECTOTYPES. 1 ♂, 2 ♀♀, same data as lectotype.

MATERIAL EXAMINED. Lectotype series of *D. distinctus* as designated above (deposited in the Ferris collection at the University of California, Berkeley); holotype ♀ of *D. orientalis* (in Dr Eichler's collection); 19 ♂♂, 18 ♀♀ ex *Collocalia esculenta*, Ampang, Kuala Lumpur, Malaya (H. E. McClure, 19.viii.1964. USNM); 2 ♂♂ ex *Collocalia esculenta cyanoptila*, Fraser's Hill, Malaya (R. Traub, 14.i.1956. USNM); 1 ♂ ex *Collocalia esculenta*, Kasiqui, British North Borneo (7.ix.1960. USNM); 1 ♀ ex *Collocalia esculenta desiderata*, Rennel Islands (15.x.1951. BMNH); 7 ♂♂, 3 ♀♀ ex *Collocalia esculenta*, Imonda, c.40 miles South of Vanimo, New Guinea (W. B. Hitchcock, 2.v.1965. BMNH); 1 ♂ ex *Collocalia* sp., New Hebrides (25.iii.1934. GBT); 1 ♀ ex "Swallow", Kediri, Java (30.vi.1937. GBT).



Figs 3-7. *Dennyus (Collodennyus) distinctus* Ferris, 1916. 3. Dorsal head setae. 4. Male, sternite II. 5. Female, sternite II. 6. Male, genital armature. 7. Male, genital sclerite.

## Discussion

Ferris (1916:311) describes the type series of *Dennyus distinctus* as "Two males, a female and two immature forms from *Collocalia* sp. (Samarang, Java, E. Jacobson coll.)". In the Ferris collection at the University of California is a series of syntypes comprising 1 ♂, 3 ♀♀ and 2 nymphs on three slides, all with the same host and locality data. It appears therefore that Ferris made an error in listing the specimens he examined.

Lord Medway (*in litt.*) informed me that the collection locality is Semarang by modern spelling, and that further information about Jacobson's material might be found in the Rijksmuseum van Natuurlijke Historie, Leiden. Writing from Leiden, Dr C. Smeenk advised: "... we have 4 specimens of *Collocalia esculenta linchi* Horsfield and Moore, collected by Jacobson at Semarang, Java, in December, 1909".

The type series of *D. distinctus* is in good condition and the specimens agree in every respect with the excellent series (see above) from *Collocalia esculenta* from Malaya. There is thus strong evidence that Ferris' material came from *Collocalia esculenta linchi*.

*Dennyus orientalis* Büttiker, 1954 was described from females only, collected from *Collocalia esculenta stresemanni*. In his description Büttiker makes no reference to *distinctus*, nor does the holotype female of *orientalis*, made available to me by Dr Eichler, show any differences from *distinctus* as defined above.

Ferris (1932) examined 1 ♂, 2 ♀♀ from *Collocalia ocista*, and published a "re-description" of *D. distinctus* based on this material. I have seen a male and a female of this series; they are not *distinctus* and Ferris' record is a misidentification. The material from *Collocalia ocista* will be described as a new species below.

Carriker (1949) mentions a single male of "*Dennyus distinctus*" from *Collocalia inexpectata bartschi*. Examination of the specimen has shown that it is not *distinctus*, but belongs to a group in which the males cannot be identified satisfactorily at present; it is listed together with other unidentifiable material at the end of this section.

### *Dennyus (Collodennyus) medwayi* spec. nov., figs 8—11

Type-host: *Collocalia gigas* (Hartert & Butler).

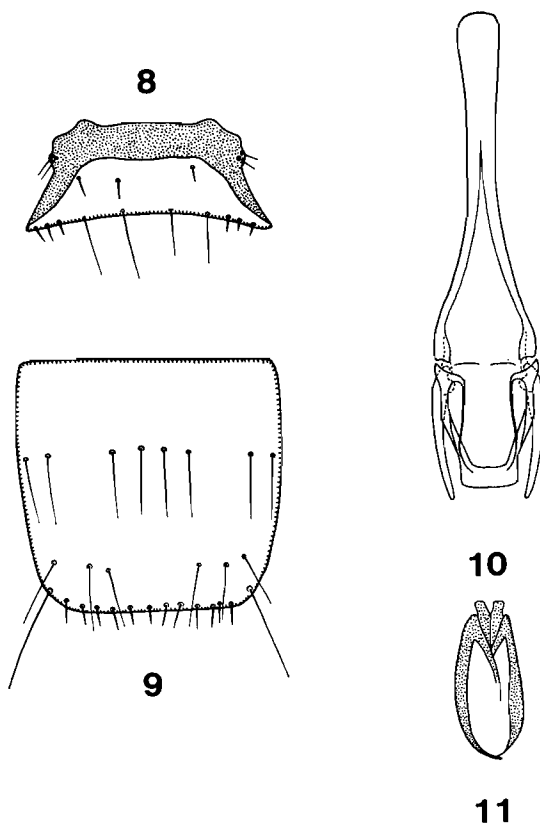
**FEMALE.** Head larger than in *distinctus*; fewer tergocentrals on I–VI; plate on sternite II broader in central part; subgenital plate lacks additional central group of setae. 7–9 central metasternal, 8–9(9) metanotal marginal setae. Characters of head and thorax otherwise as for *distinctus*.

**Tergocentrals.** I, 7–10(8); II, 8–9(8); III and IV, 8–10(9); V, 8–9(9); VI, 9–10(10); VII, 8–9(9); VIII, 6–8(7). Terminal tergite as for *distinctus*.

**Ventral chaetotaxy.** II, 8–11(9) *m*, 3–5(4) *a* (see fig. 8); III, 12–13(13) *m*, 2–7(3) *a*; IV, 12–18(15) *m*, 8–11(9) *a*; V, 4–6(6) *m*, 0–1(0) *a*, lateral brushes 28–35; VI, 4–5(4) *m*, 0 *a*, lateral brushes 20–24. Subgenital plate as in fig. 9; vulval margin with 12 stout setae (1 specimen 15); central group of setae absent (1 specimen with 1 alveolus here); other characters as for *distinctus*.

**MALE.** Similar to *distinctus* in most respects; head longer; fewer tergocentrals on I–IV; genital armature narrower; mesosomal plate and parameres more elongate; sclerite of different shape. 7, 9 central metasternal, 8 metanotal marginal setae.

**Tergocentrals.** I, 6, 7; II, 7, 8; III, 8; IV, 9, 10; V–VII, 10; VIII, 8. Terminal tergite as for *distinctus*.



Figs 8-11. *Dennyus (Collodennyus) medwayi* spec. nov. 8. Female, sternite II. 9. Female, subgenital plate. 10. Male, genital armature. 11. Male, genital sclerite.

*Ventral chaetotaxy.* II, 6,8 m, 3,4 a; III, 10 m, 3,4 a; IV, 10,11 m, 2,4 a; V, 5,6 m, 0 a, lateral brushes 28-37; VI, 4,5 m, 0 a, lateral brushes 17-20; VII, 8,9 m; VIII, 6 m. Terminally 4 submarginal, 16,20 marginal, 8 internal anal setae. Genital armature as in fig. 10, sclerite as in fig. 11.

#### DIMENSIONS.

	<i>Female</i>	<i>Male</i>
Preocular width . . . .	0.44-0.46 (0.45)	0.42, 0.43
Temple width . . . .	0.59-0.60 (0.59)	0.55
Head length . . . .	0.50-0.51 (0.50)	0.48, 0.49
Total length . . . .	2.5-2.6 (2.5)	2.1

**HOLOTYPE.** ♀ ex *Collocalia gigas*, Fraser's Hill, Pahang, Malaya (Lord Medway, 20.x.1968).



PARATYPES. 2 ♂♂, 3 ♀♀, same data as holotype.

The holotype and 1 ♂, 2 ♀♀ paratypes have been deposited at the British Museum (Natural History); 1 ♂, 1 ♀ paratypes at the South African Institute for Medical Research.

## Discussion

Both sexes of *D. medwayi* are distinguished from *D. distinctus* by having fewer tergocentral setae on the anterior tergites; the male is further distinguished by the characters of the genitalia and the female by the chaetotaxy of the subgenital plate.

The type-host *Collocalia gigas* is described by Medway (1966) as "the largest and rarest of swiftlets". The specimens upon which the new taxon is based were collected from a bird captured alive in a mist-net at a flood-lit radio station in Malaya. Further details about the bird's behaviour in captivity, especially with regard to the lack of echolocation ability, and a discussion on the taxonomic implications of the latter, have been published by Medway & Wells (1969).

I have pleasure in naming the new species in honour of Lord Medway, both as a token of recognition for his work on *Collocalia*, and in appreciation of the friendly assistance he has given me in the preparation of this paper.

## *Dennyus (Collodennyus) elliotti* spec. nov., fig. 12

Type-host: *Collocalia whiteheadi* Ogilvie-Grant.

This and the following two species are distinguished in the female by the presence of internal anal setae. Separation of males has been found somewhat difficult.

**FEMALE.** Characters of head, thorax and pleurites as for *distinctus*. 4 mesosternal, 6–10 central metasternal, 8–9 metanotal marginal setae. Abdomen as in fig. 12.

**Tergocentrals.** I, 6–8(7); II, 7–9(8); III, 8–9(8); IV & V, 9–10(10); VI, 8–10(9); VII, 9–10(9); VIII, 6–8(8).

**Ventral chaetotaxy.** II, 8–9(8) m, 5–7(6) a; III, 10–11(11) m, 3–5(4) a; IV, 10–12(11) m, 4–8(6) a; V, 4–6(5) m, 0 a, lateral brushes 30–38; VI, 2–4(3) m, 0 a, lateral brushes 9–12. Vulval margin 11–15(13) stout setae; central group 1–2(1) short setae.

**MALE.** Similar to *D. medwayi*; all dorsal and ventral setal counts overlap in the two species; temple appears to be slightly narrower in *elliotti*.

**Tergocentrals.** I, 5–8(7); II, 6–8(7); III, 6–11(8); IV, 8–10(9); V, 9–10(10); VI, 6–10(9); VII, 8–10(10); VIII, 8–9(9).

**Ventral chaetotaxy.** II, 7–11(9) m, 2–8(5) a; III, 6–9(8) m, 1–4(3) a; IV, 8–11(10) m, 2–8(4) a; V, 4–5(5) m, 0 a, lateral brushes 28–35; VI, 3–4(4) m, 0 a, lateral brushes 7–16; VII, 7–9(8) m, VIII, 6–7(6) m. Terminally, 16–20 marginal, 6–8(8) internal anal setae. Genitalia as for *medwayi*; no differences can be found in shape of sclerite.

## DIMENSIONS

	Female	Male
Preocular width . . . . .	0.42–0.45 (0.43)	0.38–0.41 (0.39)
Temple width . . . . .	0.53–0.58 (0.55)	0.50–0.53 (0.51)
Head length . . . . .	0.47–0.53 (0.49)	0.44–0.48 (0.45)
Total length . . . . .	2.5	2.0–2.1 (2.1)

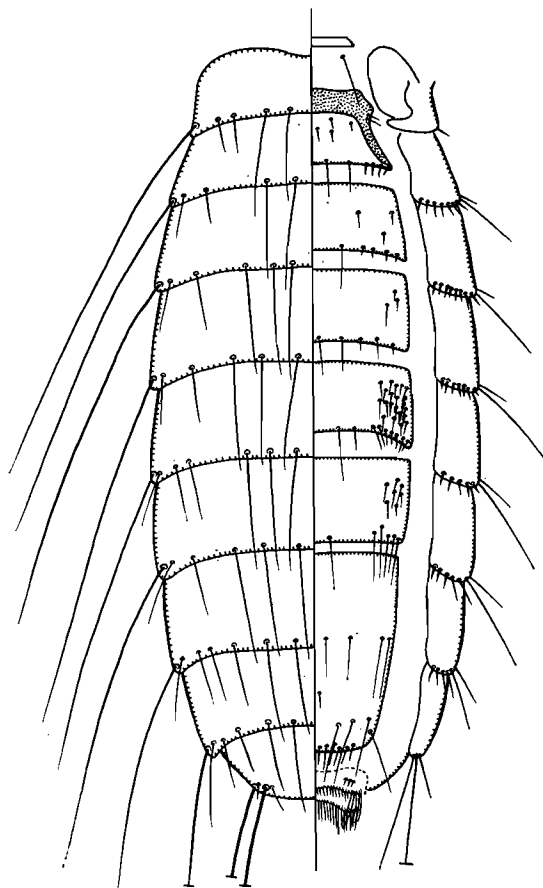


Fig. 12. *Dennyus (Collodennyus) elliotti* spec. nov. Female abdomen, dorsal/ventral view.

**HOLOTYPE.** ♀ ex *Collocalia whiteheadi*, Dalton Pass, Nueva Vizcaya, Philippine Islands (20.i.1966).

**PARATYPES.** 4 ♂♂, 1 ♀ ex *Collocalia whiteheadi*, same locality as holotype (H. E. McClure, 29.xi.1964); 2 ♂♂ ex *Collocalia whiteheadi*, Sinipsip, Benquet, Philippine Islands (29.viii.1965); 1 ♀ ex *Collocalia whiteheadi*, Kabigaan, Palawan, Philippine Islands (H. E. McClure, 8.iv.1965).

The holotype and 4 ♂♂ paratypes have been deposited at the United States National Museum; 2 ♂♀, paratypes in the collection of Dr K. C. Emerson.

### Discussion

*D. elliotti* is immediately distinguished in the female by the presence of internal anal setae; the male, however, cannot at present be separated from that of *D. medwayi*.

The new species is named in honour of Dr H. Elliott McClure, who collected a large part of the material studied during the preparation of this paper, and under whose direction the Migratory Animal Pathological Survey has done much excellent work on avian parasites in the Far East.

***Dennyus (Collodennyus) emersoni* spec. nov., fig. 13**

Type-host: *Collocalia brevirostris* (Horsfield).

Females of this species resemble *D. elliotti* in having internal anal setae, but can be separated by the greater number of tergo-centrals on I–VII. The single male in the type series does not show any reliable characters which might serve to separate it from *medwayi* and *elliotti* at present.

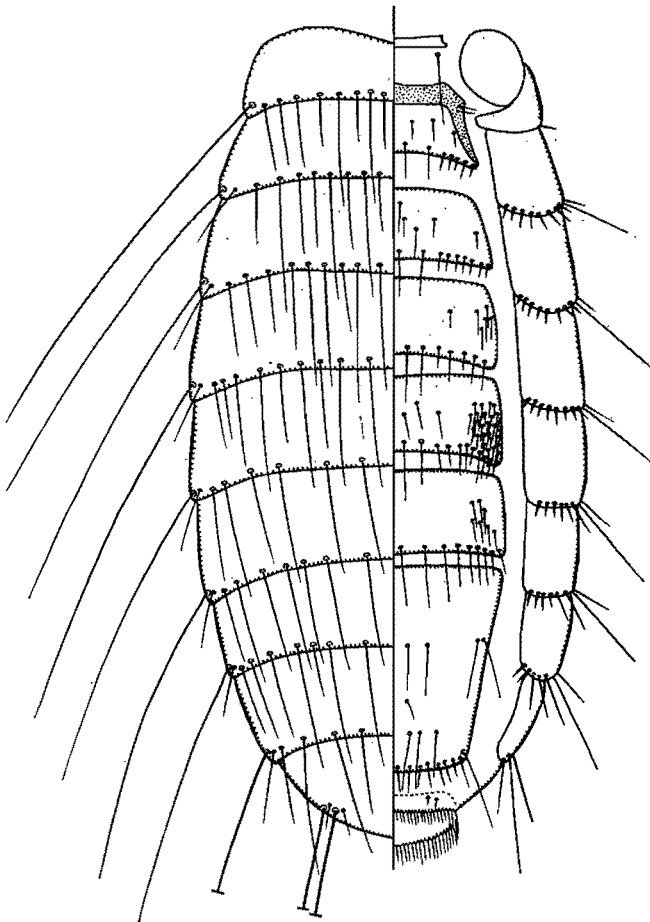


Fig. 13. *Dennyus (Collodennyus) emersoni* spec. nov. Female abdomen, dorsal/ventral view.

**FEMALE.** 4 mesosternal, 9–13(11) central metasternal, 8–10(8) metanotal marginal setae. Abdomen as in fig. 13.

*Tergocentrals.* I, 16–18(17); II, 16–19(18); III, 16–17(17); IV, 13–18(17); V, 14–17(15); VI, 13–16(14); VII, 11–13(13); VIII, 8. Terminal segment as for preceding species.

*Ventral chaetotaxy.* II, 12–18(14) *m*, 6–9(8) *a*; III, 11–16(15) *m*, 8–13(10) *a*; IV, 16–18(17) *m*, 15–22(18) *a*; V, 6–8(7) *m*, 2–8(5) *a*, lateral brushes 35–48; VI, 5–6(5) *m*, 1–4(2) *a*, lateral brushes 13–21. Vulval margin 10–15(13) stout setae, central group 1–3(2) on subgenital plate. 1–3 internal anal setae each side.

**MALE.** 4 mesosternal, 6 central metasternal, 9 metanotal marginal setae.

*Tergocentrals.* I, 8; II & III, 9; IV–VI, 10; VII, 9; VIII, 8.

*Ventral chaetotaxy.* II, 9 *m*, 6 *a*; III & IV, 12 *m*, 7 *a*; V, 4 *m*, 1 *a*, lateral brushes 32 and 36; VI, 4 *m*, 0 *a*, lateral brushes 16 and 17; VII, 8 *m*; VIII, 6 *m*. Terminally 12 marginal, 8 internal anal setae. Genital armature as for *elliotti*, sclerite distorted in only available specimen.

#### DIMENSIONS.

	Female	Male
Preocular width . . . .	0.44–0.45 (0.44)	0.41
Temple width . . . .	0.57–0.59 (0.58)	0.52
Head length . . . .	0.48–0.49 (0.48)	0.44
Total length . . . .	2.5–2.6 (2.5)	2.0

**HOLOTYPE.** ♀ ex *Collocalia brevirostris*, Doi Pha Hom Pok, Chiangmai, Thailand (MAPS, 28.x.1965).

**PARATYPES.** 2 ♀♀, same data as holotype; 1 ♂, 2 ♀♀ ex *Collocalia brevirostris*, Chiang Dao, Chiangmai, Thailand (MAPS, 25.viii.1965).

The holotype and 3 ♀♀ paratypes have been deposited at the United States National Museum; 1 ♂ 1 ♀, paratypes in the collection of Dr K. C. Emerson.

#### Discussion

*D. emersoni* has almost twice as many tergocentral setae on the anterior segments as *D. elliotti* in the female. Males of the two species are not presently separable, nor can they be distinguished from those of *D. medwayi*.

The new species is named for Dr K. C. Emerson, who kindly made available much material from his collection of Mallophaga for this study.

#### *Dennyus (Collodennyus) ferrisi* spec. nov., figs 14–17

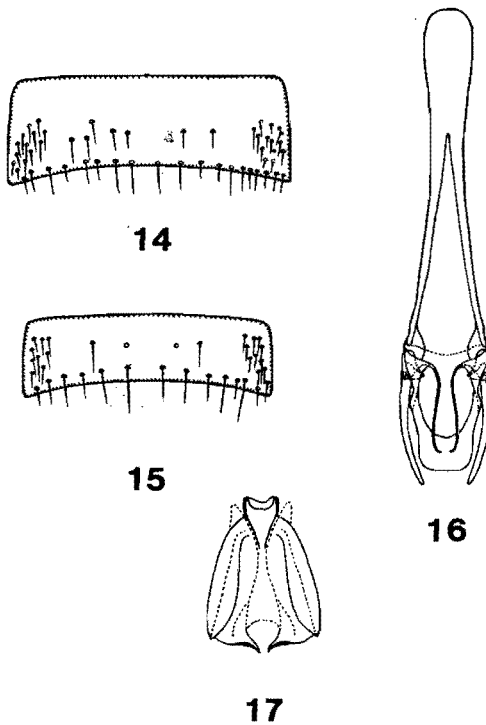
**Dennyus distinctus** Ferris, 1932 (*nec* Ferris, 1916), *Bull. Bernice P. Bishop Mus.* 98: 56, figs 9 and 10. Host: *Collocalia ocista*.

Type-host: *Collocalia leucophaea ocista* Oberholser.

**FEMALE.** 4 mesosternal, 8 central metasternal, 11 metanotal marginal setae.

*Tergocentrals.* I, 19; II, 20; III, 16; IV, 18; V, 15; VI, 14; VII, 14; VIII, 10.

*Ventral chaetotaxy.* II, 15 *m*, 7 *a*; III, 16 *m*, 18 *a*; IV, 19 *m*, 35 *a* (see fig. 14); V, 8 *m*, 7 *a*, lateral brushes 54 and 58; VI, 5 *m*, 3 *a*, lateral brushes 25 and 28. Vulval



Figs 14–17. *Dennyus (Collodennyus) ferrisi* spec. nov. 14. Female, sternite IV. 15. Male, sternite IV. 16. Male, genital armature. 17. Male, genital sclerite.

margin 13 stout setae, subgenital plate otherwise as for *emersoni*; 4+4 internal anal setae.

MALE. 4 mesosternal, 9 central metasternal, 10 metanotal marginal setae.

*Tergocentrals*. I, 16; II and III, 13; IV, 15; V, 14; VI and VII, 13; VIII, 10.

*Ventral chaetotaxy*. II, 11 *m*, 5 *a*; III, 13 *m*, 10 *a*; IV, 13 *m*, 24 *a* (see fig. 15); V, 6 *m*, 0 *a*, lateral brushes 44; VI, 4 *m*, 0 *a*, lateral brushes 21 and 23; VII, 9 *m*, 1 *a*; VIII, 6 *m*. 9 internal anal setae, other setae of terminal segment unclear. Genital armature as in fig. 16; sclerite as in fig. 17; hook-like posterior projections distinct.

#### DIMENSIONS.

	<i>Female</i>	<i>Male</i>
Preocular width . . . .	0.47	0.45
Temple width . . . .	0.62	0.58
Head length . . . .	0.51	0.49
Total length . . . .	2.9	2.2

HOLOTYPE. ♀ ex *Collocalia ocista*, Vaipae Valley, Uahuka, Marquesas Islands (Adamson, 22.ix.1929).

PARATYPE. 1 ♂, same data as holotype.

Both slides have been deposited in the Ferris collection at the University of California, Berkeley.

## Discussion

The female of *D. ferrisi* is close to *D. emersoni* in having internal anal setae and numerous tergocentrals on the anterior segments. Reliable characters for the separation of the two species must be checked when further material becomes available; the holotype female is distinguished by larger dimensions throughout, the chaetotaxy of sternite IV, and the presence of 4+4 internal anal setae. The male is separated from *medwayi*, *elliotti* and *emersoni* by the higher tergocentral counts for anterior segments, these approaching the ranges found for *distinctus*. *D. ferrisi* is larger than all four species mentioned, the chaetotaxy of sternite IV is dense and the genitalia are characteristic, this combination of characters setting the paratype male of *ferrisi* apart from all other species.

Ferris (1932) provided illustrations of the new species, incorrectly identified as *distinctus*. These are inaccurate in several respects, also failing to depict internal anal setae in the female, and indicating claws on tarsus I in both sexes; however, Ferris did note the characteristic hook-like structures in the male genital sclerite.

## ADDITIONAL MATERIAL IN THE *distinctus* SPECIES-GROUP

No attempt has been made to identify or name the following material, consisting mostly of single specimens, because of the inherent danger that they might represent stragglers or contaminations. All fall into the *distinctus* species-group according to the characters of the head.

2 ♂♂ ex *Collocalia troglodytes*, Dalton Pass, Nueva Vizcaya, Philippine Islands (H. E. McClure, 29.xi.1964. KCE); 1 ♂ ex *Collocalia hirundinacea*, Sibil Valley, Netherlands New Guinea (L. Quate, 21.x.1961. KCE); 1 ♂ ex *Collocalia inquieta ponapensis*, Ponape, East Carolines (L. P. Richards, 26.xii.1947. USNM); 1 ♂ ex *Collocalia inexpectata bartschi*, Guam Island (R. Baker, 29.vii.1945. USNM); 1 ♂ ex *Collocalia maxima lowi*, Meraja Cave, Bau, Sarawak (26.vii.1957. BMNH); 1 ♂ ex *Collocalia f. fuciphaga*, Karangduwur Cave, Kebumen, Central Java (Medway, 16.vi.1961. BMNH); 1 ♀ ex *Collocalia fuciphaga vestita*, Lembong Cave, Sarawak (14.xi.1957. BMNH).

## THE *thompsoni* SPECIES-GROUP

*Dennyus* (*Collodennyus*) *franciscus* Thompson, 1941, figs 18–21

**Dennyus franciscus** Thompson, 1941, *Ann. Mag. nat. Hist.* (11) 7: 530, plate vii, figs 1 and 2, text-fig. 1a. Type-host: *Collocalia francica reichenowi* (= *C. spodiopygia reichenowi* Stresemann).

**FEMALE.** General appearance and chaetotaxy as in fig. 18. Head characteristically shaped, lateral margins of forehead between *dhs* 8 and 4–5 strongly concave. Dorsal head setae as in fig. 19. Important features: 3 about  $\frac{1}{4}$  length of 2; 4 short and stout; 5 large and peg-like; 8 borne on a raised tubercle; 13 short, just reaching alveolus of 16. Thorax with 4 mesosternal, 6–10(8) central metasternal and 8–9(8) metanotal marginal setae. Abdomen short and rounded, paratergites rather narrower than in *distinctus* species-group, but chaetotaxy essentially the same.

*Tergocentrals.* I, 6–9(8); II, 10–13(11); III–VI, 11–14(13); VII, 11–13(12);

VIII, 8-10(9), long on all segments; short setae associated with postspiraculars long on posterior tergites. Terminally, the normal 2 stout setae each side with 1 minute seta between alveoli; additionally 2 or 3 short setae medially each side (replacing the invariably single minute seta of the *distinctus* species-group).

*Ventral chaetotaxy.* II, 7-11(9) *m*, 4-6(5) *a*; III, 10-12(11) *m*, 6-10(8) *a*; IV, 12-16(14) *m*, 6-12(9) *a*; V, 6-8(8) *m*, 2-3(3) *a*, lateral brushes 25-35; VI, 5-6(6) *m*, 1-4(2) *a*, lateral brushes 16-24. Vulval margin with 14-16(15) setae, subgenital plate with usual 4+4 in posterior corners, middle region with usual 2+4+2 (3 and 4 laterally observed in 2 specimens) and a central group of 3-5(4) setae. 2-4 internal anal setae each side.

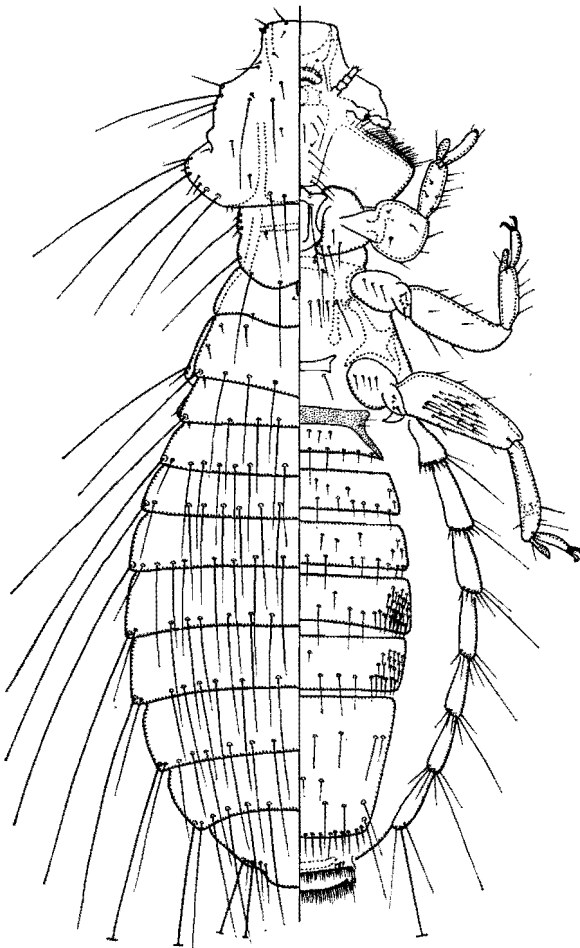


Fig. 18. *Dennyyus* (*Collodennyyus*) *francicus* Thompson, 1941. Female, dorsal/ventral view.

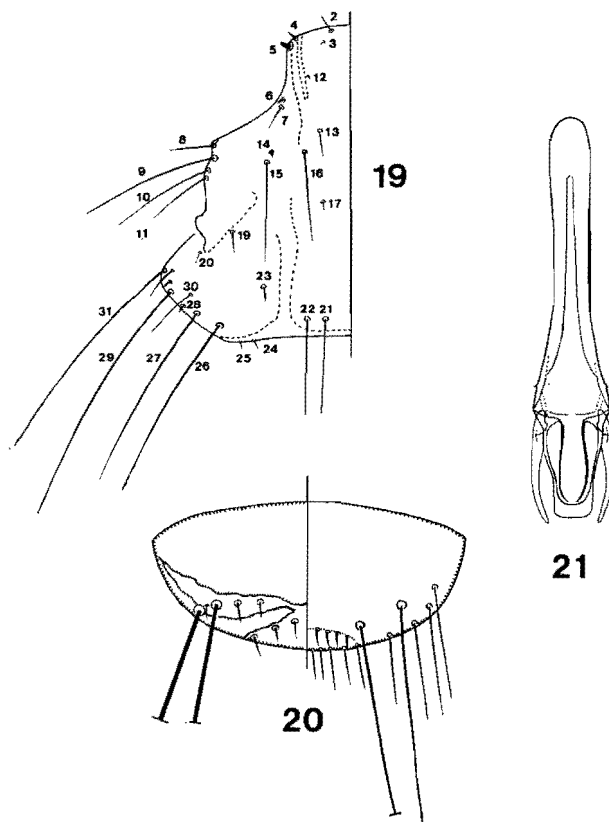
MALE. Head, thorax and paratergites as for female. 7 central metasternal, 7 metanotal marginal setae.

*Tergocentrals.* I, 6; II, 9; III, 12; IV, 13; V, 15; VI and VII, 13; VIII, 11. Terminal segment as in fig. 20; a distinct break in sclerotisation visible; 6 dorsal anal setae.

*Ventral chaetotaxy.* II, 6 m, 6 a; III, 9 m, 8 a; IV, 10 m, 5 a; V, 6 m, 3 a, lateral brushes 21 and 27; VI, 4 m, 3 a, lateral brushes 16 and 11; VII, 9 m, 1 a; VIII, 6 m. Terminal segment as in fig. 20; 14 marginal, 4 submarginal, 9 internal anal setae. Genital armature as in fig. 21, sclerite distorted in the single male available.

# DIMENSIONS.

	Female	Male
Preocular width . . . .	0.41-0.42 (0.41)	0.38
Temple width . . . .	0.53-0.55 (0.42)	0.50
Head length . . . .	0.42-0.43 (0.42)	0.41
Total length . . . .	2.0-2.1 (2.1)	1.7



Figs 19-21. *Dennyus (Collodennyus) francicus* Thompson, 1941. 19. Dorsal head setae. 20. Male, terminal abdominal segment, dorsal/ventral. 21. Male, genital armature.



**MATERIAL EXAMINED.** The above description is based on the entire type series of *D. francicus*, i.e. ♀ holotype, ♂ allotype, 4 ♀♀ paratypes ex "*Collocalia francica* (Gm) (Grey Martin)", Malaupaina, Three Sisters, British Solomon Islands (R. A. Lever, 12.v.1934. GBT).

In addition, the following specimens were also identified as *D. francicus*: 1 ♂ ex *Collocalia hirundinacea*, Sibil Valley, Netherlands New Guinea (L. Quate, 21.xi.1961. KCE); 1 ♀ ex *Collocalia hirundinacea*, Bokondini, Netherlands New Guinea (L. Quate, 19.xi.1961. KCE).

Apart from slight variation in setal counts and minor size differences, this pair of specimens agreed in every respect with the type series of *D. francicus*.

## Discussion

*D. francicus* is a distinctive species, characterised by the shape and chaetotaxy of the head, the short, rounded abdomen and the chaetotaxy of the terminal tergite in both sexes. Little can be said at this stage about the apparent presence of *francicus* on *Collocalia hirundinacea* until this is confirmed by further collections.

The choice of specific epithet for this louse was rather unfortunate. The name *francica* is one of the older available among *Collocalia* and has at times been in use as a specific epithet for large groups of swiftlets (Medway, 1966). The Mallophaga of *Collocalia francica* (Gmelin), found on the Indian Ocean islands of Mauritius and Reunion, are as yet unknown. For this reason I feel that to name as the "*francicus* species-group" those *Dennyus* which are apparently related to *francicus* might lead to some misunderstanding, or implication that certain *Collocalia* taxa are related in some way to *C. francica*, when in fact there is no evidence to this effect. I have therefore chosen *thompsoni* in preference to *francicus* as the name of the species-group.

## *Dennyus (Collodennyus) thompsoni* spec. nov., figs 22–25

Type-host: *Collocalia maxima lowi* Sharpe.

**FEMALE.** Head shape and chaetotaxy as for *francicus*, except that the preocular angles are more smoothly rounded and *dhs* 8 is not borne on a raised tubercle. 6 mesosternal, 8–12(10) central metasternal and 8 metanotal marginal setae. Abdomen as in fig. 22, elongated, with a wide anal corona.

**Tergocentrals.** I, 7–9(8); II, 9–10(10); III, 10–12(11); IV, 10–11(10); V, 10–13(12); VI, 10–12(11); VII, 10–14(12); VIII, 10. Terminal segment dorsally as for *distinctus* species-group, with 2 stout and 2 minute setae each side.

**Ventral chaetotaxy.** II, 5–7(6) *m*, 5–10(8) *a*; III, 10–11(10) *m*, 8–12(10) *a*; IV, 11–13(12) *m*, 12–24(19) *a*; V, 4–6(5) *m*, 5–11(9) *a*, lateral brushes 36–43; VI, 4–6(5) *m*, 3–6(5) *a*, lateral brushes 23–26. Vulval marginal setae 18–21(20), subgenital plate with usual 4+4 in posterior corners, middle region with usual 2+4+2, 1 central seta. 1–4 internal anal setae each side.

**MALE.** Head and thorax as for female. 5–8(6) mesosternal, 8–9(9) central metasternal and 8 metanotal marginal setae.

**Tergocentrals.** I, 6–8(7); II, 7–9(8); III, 8–10(8); IV, 10–11(10), V, 9–10(10); VI, 11–13(12); VII, 12–15(14); VIII, 13–15(14). Tergocentrals of VII and VIII crowded together laterally (see fig. 23). Terminal segment as for *distinctus* species-group; 6 dorsal anal setae.

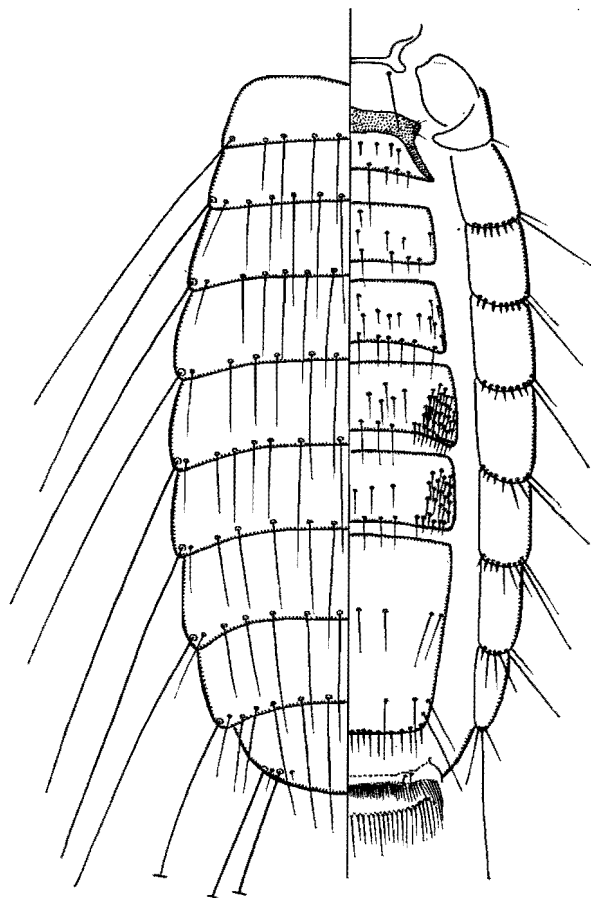


Fig. 22. *Dennyus (Collodennyus) thompsoni* spec. nov. Female abdomen, dorsal/ventral.

*Ventral chaetotaxy.* II, 4-5(5) *m*, 4-7(6) *a*; III, 6-8(7) *m*, 6-10(8) *a*; IV, 8-10(9) *m*, 9-14(11) *a*; V, 4 *m*, 2-6(4) *a*, lateral brushes 27-34; VI, 4 *m*, 1-3(2) *a*, lateral brushes 17-24; VII, 6-8(7) *m*, 0-1(0) *a*; VIII, 6 *m*. Terminal segment with 15-18(16) marginal, 4 submarginal and 6-8(8) internal anal setae. Genital armature without any unusual features (fig. 24); sclerite distinctive, genital sac with large denticles (fig. 25).

#### DIMENSIONS.

	<i>Female</i>	<i>Male</i>
Preocular width . . . . .	0.43-0.44 (0.44)	0.40-0.42 (0.41)
Temple width . . . . .	0.57-0.58 (0.57)	0.52-0.55 (0.53)
Head length . . . . .	0.47	0.42-0.46 (0.45)
Total length . . . . .	2.4-2.5 (2.4)	1.9-2.1 (2.0)

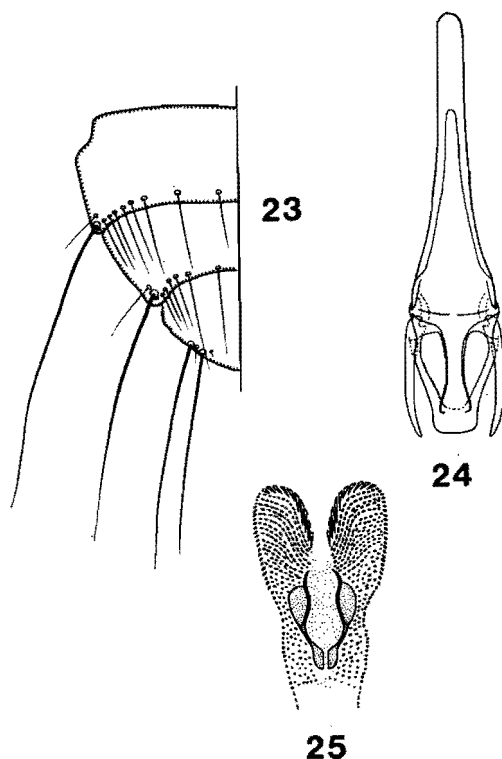
HOLOTYPE. ♀ ex *Collocalia maxima lowi*, Meraja Cave, Bau, Sarawak (26.vii.1957)

PARATYPES. 4 ♂♂, 2 ♀♀, same data as holotype.

All type material has been deposited at the British Museum (Natural History), London.

## Discussion

*D. thompsoni* appears to be related to *D. francicus*, according to the characters of the head. The female is distinguished by the elongated abdomen with wide anal corona and the chaetotaxy of the terminal tergite—the characters of the abdomen are in fact more reminiscent of the *distinctus* species-group than of *D. francicus*. The male abdomen is notable for the crowded tergocentrals laterally on VII and VIII, and the shape of the genital sclerite, both features setting this species apart from all other *Collodennys* examined.



Figs 23–25. *Dennyus (Collodennys) thompsoni* spec. nov. 23. Male, terminal abdominal tergites. 24. Male, genital armature. 25. Male, genital sclerite.

I have pleasure in naming the new species for Mr Gordon B. Thompson, in appreciation for lending me valuable type material for this study.

The type series of *D. thompsoni* was chosen from *Collocalia maxima lowi*, the specimens from this host being in good condition for detailed study. Material was also seen from three other species of *Collocalia* (listed below), and it proved impossible to separate these specimens taxonomically from the series from *C. maxima lowi*.

4 ♂♂, 1 ♀ ex *Collocalia v. vanikorensis*, Abagua Cave, near Tigoa, Rennel Islands (Torben Wolff, 21.iii.1965. BMNH); 2 ♂♂, 1 ♀ ex *Collocalia whiteheadi*, Kabigaan, Aborlan, Palawan, Philippine Islands (H. E. McClure, 8.iv.1965. KCE); 1 ♂♀ ex *Collocalia whiteheadi*, Dalton Pass, Nueva Vizcaya, Philippine Islands (H. E. McClure, 29.xi.1964. KCE); 4 ♂♂, 2 ♀♀ ex *Collocalia brevirostris*, Kanchanaburi, Tha Kanun, Hien Laem, Thailand (R. Elbel and H. Deignan, 20.xi.1953. KCE and USNM); 1 ♂ ex *Collocalia brevirostris*, Doi Pha Hom Pok, Chiangmai, Thailand (MAPS, 28.x.1965. USNM).

All the material listed above has been labelled as *D. thompsoni sens. lat.* The host information is rather confusing, and might be partly due to host misidentifications or incorrect labelling of slides, yet the number of specimens involved seems to rule out the possibility of straggling. It is clear that further collections must be made to confirm that *D. thompsoni sens. lat.* does occur naturally on *C. vanikorensis*, *whiteheadi* and *brevirostris* (as well as confirmation that the choice of *C. maxima lowi* as type-host is justified). If this is so, more refined taxonomic methods, statistical analysis or biological information might show that the different populations can be separated, but until such time they should be regarded as *thompsoni sens. lat.* It should be stressed that apart from a slight size difference in the females from *C. whiteheadi*, all characters considered to be of taxonomic value overlap in the different populations; the males all have the same arrangement of tergoventral setae on VII and VIII, and the same type of sclerite in the genital sac.

### Key to the species of *Collodennys*

- |   |                                   |
|---|-----------------------------------|
| 1 Lateral margin of forehead between <i>dhs</i> 8 and 4-5 almost straight; <i>dhs</i> 5 short and slender ( <b>distinctus</b> species-group)  | 2                                 |
| - Lateral margin of forehead between <i>dhs</i> 8 and 4-5 strongly concave; <i>dhs</i> 5 stout and peg-like ( <b>thompsoni</b> species-group) | 9                                 |
| 2 Males   | 3                                 |
| - Females   | 5                                 |
| 3 More than 13 tergoventral setae on I and II   | 4                                 |
| - Less than 10 tergoventral setae on I and II   | <b>medwayi, ellioti, emersoni</b> |
| 4 Genital sclerite with hook-like projections (fig. 17); 24 anterior setae on sternite IV (one specimen)                                      | <b>ferrii</b>                     |
| - Sclerite without hook-like projections (fig. 7); 9 or less anterior setae on sternite IV  | <b>distinctus</b>                 |
| 5 Internal anal setae absent  | 6                                 |
| - Internal anal setae present   | 7                                 |
| 6 15 or more tergoventral setae on I and II   | <b>distinctus</b>                 |
| - 10 or less tergoventral setae on I and II   | <b>medwayi</b>                    |
| 7 13 or more tergoventral setae on I and II   | 8                                 |
| - 10 or less tergoventral setae on I and II   | <b>ellioti</b>                    |
| 8 35 anterior setae on sternite IV (1 specimen)   | <b>ferrii</b>                     |
| - 22 or less anterior setae on sternite IV  | <b>emersoni</b>                   |
| 9 Terminal segment dorsally with 1-3 short setae mediad to normal 2 stout+1 minute setae each side; abdomen short and rounded                 | <b>francisci</b>                  |
| - Terminal segment dorsally with only 1 minute seta mediad to normal 2 stout+1 minute setae each side; abdomen elongated                      | <b>thompsoni</b>                  |

## HOST-PARASITE RELATIONSHIPS

The preliminary nature of this study must be stressed, as there is insufficient material from a suitably wide range of hosts upon which to base any definite statements regarding host-relationships. However, tentative suggestions regarding the affinities of three forms of *Collocalia* will be put forward below.

In *Collodennyus* there appear to be two main lines of development, represented by the *distinctus* and *thompsoni* species-groups. Of the two species at present placed in the *thompsoni* group, *franciscus* shows some unusual features not encountered in other species of *Collodennyus*. *D. thompsoni*, on the other hand, while having the same type of head as *franciscus*, has abdominal characters which are more reminiscent of the *distinctus* group; again, however, the male has certain features which set it apart from all other species. It is of interest to note that echolocation has been recorded from *C. spodiopygia terrareginae* and *C. maxima lowi* (see Medway, 1966). A race of the former is the type-host of *D. franciscus*, while the latter is the type-host of *D. thompsoni*.

*Collocalia gigas*

Medway (1966) provisionally associated *C. gigas* (then untested for echolocation ability) with the echolocating "grey" group of swiftlets, on morphological grounds. Medway & Wells (1969) found that *C. gigas* was incapable of echolocation, and attempted to explain this by proposing two alternatives: "that *C. gigas*, as a member of a monophyletic 'grey' swiftlet group, has secondarily lost the ability to echolocate . . . , or that *C. gigas*, evolving independently from an ancestral non-echolocating stock, has acquired features convergent with those of the 'grey' swiftlets". The characters of *D. medwayi* indicate that it is related to *D. distinctus* from *Collocalia esculenta*, a member of the "glossy" group of swiftlets which has been found to be incapable of echolocation (Medway, 1966). The parasitological evidence therefore supports the second of Medway and Wells' proposals, i.e., that *gigas* is evolved from the same ancestral stock as *esculenta* (the "glossy" group), lacks the ability to echolocate, yet has secondarily acquired certain morphological features in common with the "grey" group.

*Collocalia brevirostris* and *C. whiteheadi*

Peters (1940) regards *whiteheadi* as a distinct species, while Medway (1966) treats this form as a race of *brevirostris*. The *Collodennyus* material available is rather confusing. *D. thompsoni sens. lat.* has been recorded from both forms, as well as two new species belonging to the *distinctus* species-group, *D. elliotti* from *whiteheadi* and *D. emersoni* from *brevirostris*. Based on the latter evidence alone, one would be inclined to suggest that *whiteheadi* and *brevirostris* are specifically distinct, but the apparent presence of *D. thompsoni sens. lat.* is a complicating factor, and further collecting must be done before putting forward any suggestions of this nature. Furthermore, if *elliotti* and *emersoni* are considered to be related to *distinctus* and *medwayi* (as they are in this paper), it means that their hosts could possibly be related to the non-echolocating "glossy" group of swiftlets. Medway has positive records of the rattle call being uttered by *C. brevirostris vulcanorum* in Java; a nesting site of *C. b. brevirostris* in Sumatra is a completely dark natural tunnel several miles long, indicating that this form must also be capable of echolocation (see Medway, 1966). It is clear that considerably more work must be done on the parasites, and the echolocation ability, of the different forms assigned to *C. brevirostris* by Medway before any definite statements can be made regarding their phylogenetic affinities.

## ACKNOWLEDGEMENTS

I wish to thank the following persons for providing material, advice on several points, and friendly assistance throughout the duration of this study: Dr T. Clay, British Museum (Natural History), London; Dr K. C. Emerson, Arlington, Virginia; Drs J. A. Chemsak, B. C. Nelson and J. A. Powell, University of California, Berkeley; Mr Gordon B. Thompson, Cambridge, England; Dr O. S. Flint, United States National Museum, Washington; Lord Medway, University of Malaya, Kuala Lumpur; Dr W. Eichler, Kleinmachnow, German Democratic Republic; Dr W. Büttiker, Basle, Switzerland and Dr C. Smeenk, Leiden, Holland.

The completion of this paper was made possible by a visit to the British Museum (Natural History) during the latter part of 1969; financial assistance for this purpose from the South African Council for Scientific and Industrial Research and the South African Institute for Medical Research is gratefully acknowledged.

Finally, I wish to thank Dr F. Zumpt for his patient supervision of this work, and the Director of the South African Institute for Medical Research for providing library and research facilities.

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Manuscript received 10 April 1970.